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Life-history implications of the allometric scaling of growth

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HIGHLIGHTS

- We reformulate the biphasic growth model of Quince et al. (2008a) and generalize it to allow for non-isometric growth.
- Identical growth curves can result in widely different levels of reproductive investment.
- Fitness depends on reproductive investment, thus size is not all that matters.
- The value of the allometric scaling exponent has dramatic effects on evolutionary predictions.

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ABSTRACT

Several phenomenological descriptions, such as the von Bertalanffy growth model, have been widely used to describe size-at-age and individual growth across a diverse range of organisms. However, for modelling life histories, as opposed to just growth, biologically and mechanistically meaningful growth models, based on allocation decisions, have become increasingly important. This is because fitness is determined by survival and reproduction, which are not addressed directly in phenomenological growth models. To elucidate these considerations, we take as a starting point the biphasic growth model by Quince et al. (2008a, J. Theor. Biol. 254:197) which has the advantage that the underlying allometric scaling of net energy intake can be freely chosen. First, we reformulate this model such that individual size is given in meaningful units of length and weight, facilitating the model's interpretation and application. Second, we show that even though different allometric scaling relationships can produce practically identical growth trajectories, the accompanying reproductive investments are highly dependent on the chosen allometric exponent. Third, we demonstrate how this dependence has dramatic consequences for evolutionary predictions, in particular with regard to the age and size at maturation. These findings have considerable practical relevance, because empirically observed allometric exponents are often uncertain and systematically differ from those assumed in current standard growth models.

1. Introduction

Understanding individual growth and its determinants has intrigued ecologists for decades, and a range of growth models have been developed to assist in this task (e.g., von Bertalanffy, 1957, 1938; Charnov et al., 2001; Kozlowski, 1992, 1996; Kozlowski and Teriokhin, 1999; Lester et al., 2004; West et al., 2001). Many growth models describe average growth in a population and even individual growth reasonably well, but most of them lack a mechanistic basis in terms of energy acquisition and energy allocation (Ricklefs, 2003). This becomes a severe handicap when using growth models for addressing life-history questions (Day and Taylor 1997). Life-history theory attempts to understand and predict lifetime trajectories of survival, growth, and reproduction that maximise fitness in different environments (Ware, 1982; Roff, 2002). Growth is a major determinant of fitness, because it affects survival and reproduction, as reviewed in Arendt (1997), Enberg et al. (2012). Since reproduction directly influences fitness, it is imperative for life-history models to accurately represent reproduction in addition to survival and growth (Roff, 2002; Enberg et al., 2012).

Postnatal growth curves often have a roughly sigmoid shape (Kerkhoff, 2012) that can be described by the so-called Pütter model (Pütter, 1920). This model assumes that the change of body weight W follows the equation $dW/dt = \eta W^m - \kappa W^n$, where η, κ, m,

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and n are unknown parameters (von Bertalanffy, 1957). Subsequent researchers used variants of the Pütter equation to successfully model individual growth (Ricklefs, 2003; Banavar et al., 2002). However, most of these and other simple growth models cannot be expected to describe fitness accurately: they largely ignore reproductive investment, or assume that resources are allocated in fixed proportions to survival, growth, and reproduction (Kerkhoff, 2012; Sibly, 2012, but see Charnov et al., 2001).

The standard von Bertalanffy growth model (von Bertalanffy 1938), for instance, is a special case of the Pütter equation with $m=2/3$ and $n=1$. It is probably the mathematical description of individual growth most widely used by empiricists. Despite being broadly applied and having an almost canonical status, especially in models of fish-like growth (Froese and Pauly, 2013), the use of the von Bertalanffy model has repeatedly been criticised on biological (e.g., Day and Taylor, 1997; Knight, 1968; Roff, 1992) and statistical grounds (e.g., Roff, 1980). Among other limitations, the original derivation of the model (von Bertalanffy, 1957) did not consider trade-offs between growth and reproduction in the allocation of acquired energy, although von Bertalanffy himself pointed out that juvenile and adult growth trajectories require different parameterisation of his standard growth model ("first growth type" in von Bertalanffy, 1957). These trade-offs are also not included explicitly in most current applications of the model (for an exception, see Ohnishi et al., 2012).

If the aim is to provide a phenomenological description of a growth trajectory and stop there, these shortcomings of the Pütter model and its variants [such as the von Bertalanffy, Gompertz, and logistic growth models (Ricklefs, 1968, 2003)] do not apply. However, when a more mechanistic description of growth is needed, the limitations of these models become increasingly restrictive. In particular, several authors have argued that when modelling life-history strategies, the shape of growth trajectories should result from evolutionary adaptation, rather than being imposed a priori (Kozlowski, 1996; Day and Taylor, 1997; Czarnoleski and Kozlowski, 1998).

What alternative models are available? Measures of fitness need to account for fecundity, so mechanistically sound life-history models require at least two compartments, soma and gonads, to which acquired energy can be allocated. Various two-compartment growth models have been developed and applied in life-history theory, ranging from tractable models with few parameters, such as those of Ware (1982), Roff (1983), Kozlowski (1996), and Charnov et al. (2001), to more complex state-dependent growth models with very large numbers of evolutionarily optimised parameters [up to millions, as in, e.g., Jørgensen and Fiksen (2006)].

Here we focus on growth of iteroparous organisms with alternating periods of somatic growth and reproductive investment, which often arise due to seasonality of the environment and periodicity of reproductive events in time. Life-history theory predicts that indeterminate growth is favoured over determinate growth under such circumstances and that the relative amount of acquired energy invested into reproduction should gradually increase with age, giving rise to decelerating growth curves that approach an asymptotic size at old ages (reviewed by Roff, 2002; Heino and Kaitala, 1999; Kozlowski, 2006). Earlier work on mechanistic models of indeterminate growth, inspired by fish-like life histories, by Pauly (1981), Kozlowski (1992, 1996), Kozlowski and Teriokhin (1999), and Lester et al. (2004), resulted in a general biphasic growth model described by Quince et al. (2008a, 2008b). In our view, the latter model offers a good balance between biological realism and simplicity, in a way that makes it particularly suited for general life-history studies. First, the equations in Quince et al. (2008a) describe the growth of both somatic and gonadic tissue. Second, the model incorporates maturation as a distinct life-history transition, described by a parameter measuring an organism's age at maturation. Third, and perhaps most importantly, the model allows for a wide range of allometries of net energy acquisition with body weight, as compared to simpler growth models that assume a given allometry, typically with allometric exponents of 2/3 (e.g., Lester et al., 2004; Kooijman, 2010) or 3/4 (e.g., West et al., 2001, Brown et al., 2004).

The flexible allometric scaling of net energy acquisition, with a net-intake exponent β, is of more than theoretical interest, as it can greatly affect optimal life histories [as illustrated, e.g., by Fig. 5B in Quince et al. (2008a)]. This exponent β describes the allometric scaling of the stream of acquired net energy available for growth and reproduction to an organism, which results from the difference between two processes: energy intake and energy expenditure on metabolism. The model by Quince et al. (2008a) assumes that these two processes scale similarly with body size, i.e., the two allometric exponents of the Pütter equation are equal, $m=n=\beta$. Indeed, the allometric scaling of these two processes is often similar (Hanson et al., 1997) and can be treated as being equal for the purpose of growth models, at least for fish (Quince et al., 2008a). For example, recent meta-analyses of interspecific scaling of fish metabolic rates concluded that they scale with body mass with an average exponent of 0.75–0.88 (Clarke and Johnston, 1999; White et al., 2006; Downs et al., 2008; Makarieva et al., 2008). Studies of the intraspecific scaling of metabolic rate (which is the more appropriate scaling from the perspective of our study) in teleost fish reported a similar range, with 80% of studies falling in the range of 0.65–0.96 and a mean value of 0.80 (Clarke and Johnston, 1999; Killen et al., 2010).

Unfortunately, the commendable flexibility of the Quince et al. model may hinder its widespread application. To allow β to deviate from 2/3, the value used by Lester et al. (2004) in an otherwise nearly identical model, Quince et al. chose to measure body size in units that depend on β, instead of the more familiar units of length or weight. For $\beta=2/3$, somatic growth after maturation in the Quince et al. model collapses to the von Bertalanffy model, and body size is conveniently expressed in units of length, whereas for other values of β, the generalised body size introduced by Quince et al. has the unit of $L^{3(1-\beta)}$, where L is the unit of length. Although the conversion of this generalised body size to units of length or weight is mathematically trivial, we believe that such non-standard units hamper more widespread use of this important growth model.

The aim of this study is therefore threefold. First, we introduce an alternative formulation of the Quince et al. model in which body size is expressed in terms of natural units for length and weight. It is our hope that this more accessible formulation may contribute to a wider acknowledgement of the virtues of the flexible growth model proposed by Quince et al. Second, we highlight that, while the choice of the allometric exponent β, within reasonable limits, is not important for modelling growth trajectories, the implications of this choice for reproductive investment are profound. Third, we illustrate how this, in turn, has important consequences for optimal maturation schedules and other life-history inferences.

2. Reformulation of the growth model of Quince et al.

Here we reformulate the growth model of Quince et al. (2008a) such that the unit of size becomes length or weight, which makes the model easy to use and interpret. We also generalise the allometric scaling of body weight with body length, instead of relying on the simpler assumption of isometric scaling used by Quince et al. (2008a). Otherwise, the underlying assumptions are the same as in Quince et al. (2008a). We focus directly on the pattern of interannual growth and do not discuss the underlying

continuous growth model in detail, as the latter is already well covered by Quince et al. (2008a).

2.1. Assumptions

Briefly, the assumptions underlying the considered growth model are as follows:

1. Each year, juveniles allocate all net energy intake (i.e., their available surplus energy) to somatic growth, while in adults, a period of somatic growth is followed by a period of reproductive investment within each year (Assumption 3 in Quince et al., 2008a). We assume that an individual's size cannot decrease over time, and thus, that the net energy intake is always non-negative.
2. The rate of weight growth is allometrically related to somatic weight W according to $\mathrm{d}W/\mathrm{d}t = c\,W^{\beta}$ (Assumption 2 in Quince et al., 2008a).
3. Somatic weight is allometrically related to length L according to $W = b\,L^{\alpha}$ ($\alpha = 3$ in Quince et al., 2008a).
4. Somatic tissue is q times as costly to produce, per unit of weight, as gonadic tissue, and this ratio is independent of size (Assumption 4 in Quince et al., 2008a). The relative reproductive investment r_a, measured as the ratio of gonadic weight to somatic weight G_a/W_a at age a, varies with age: $r_a = 0$ in juveniles versus $r_a > 0$ in adults. An individual's total weight is the sum of its somatic and gonad weight, $W+G$.

We define the age a_{mat} at maturation as the age at first reproduction, so the maturation decision and the first allocation to reproduction occur between ages $a_{\mathrm{mat}}-1$ and a_{mat} Accordingly, individuals with ages $a < a_{\mathrm{mat}}$ (at the annual census) are juveniles, while those with ages $a \geq a_{\mathrm{mat}}$ are adults.

2.2. Growth model

The interannual growth in length and weight is then given by the following recurrence equations:

$$L_{a+1} = \sqrt[(1-\beta)\alpha]{\frac{L_a^{(1-\beta)\alpha} + (1-\beta)\,c b^{-(1-\beta)}}{1+q^{-1}(1-\beta)\;r_{a+1}}} \tag{1a}$$

and

$$W_{a+1} = \sqrt[1-\beta]{\frac{W_a^{1-\beta} + (1-\beta)\,c}{1+q^{-1}\,(1-\beta)\;r_{a+1}}}, \tag{1b}$$

where L_a and W_a denote the length and weight at age a.

The juvenile growth trajectory in length and weight follows from inserting $r_a = 0$ in Eqs. (1):

$$L_a = \sqrt[(1-\beta)\alpha]{L_0^{(1-\beta)\alpha} + c\,(1-\beta)\;b^{-(1-\beta)}a} \tag{2a}$$

and

$$W_a = \sqrt[1-\beta]{W_0^{1-\beta} + c\,(1-\beta)\,a}. \tag{2b}$$

While adult growth in general depends on r_a, an interesting special case occurs when the relative reproductive investment of adults is constant, i.e., $r_a = r$ for $a \geq a_{\mathrm{mat}}$. Then the adult growth trajectory in length and weight can be given in closed form,

$$L_a = \sqrt[(1-\beta)\alpha]{R^{a-a_{\mathrm{mat}}}(L_0^{(1-\beta)\alpha} + H a_{\mathrm{mat}}) + \frac{RH}{1-R}(1-R^{a-a_{\mathrm{mat}}})} \tag{3a}$$

and

$$W_a = \sqrt[1-\beta]{R^{a-a_{\mathrm{mat}}}(W_0^{1-\beta} + Hb^{1-\beta}a_{\mathrm{mat}}) + \frac{RHb^{1-\beta}}{1-R}(1-R^{a-a_{\mathrm{mat}}})}, \tag{3b}$$

where $H = c(1-\beta)\;b^{-(1-\beta)}$ and $R = [1+q^{-1}\,(1-\beta)\;r]^{-1}$. Since $R<1$, $R^{a-a_{\mathrm{mat}}}$ becomes small at old ages, and the asymptotic length and weight are given by

$$L_\infty = \sqrt[(1-\beta)\alpha]{\frac{RH}{1-R}} = \sqrt[(1-\beta)\alpha]{\frac{qc}{rb^{1-\beta}}} \tag{4a}$$

and

$$W_\infty = \sqrt[1-\beta]{\frac{RHb^{1-\beta}}{1-R}} = \sqrt[1-\beta]{\frac{qc}{r}}. \tag{4b}$$

It follows from Eqs. (1) that the maximum relative reproductive investment between ages a and $a+1$, corresponding to a complete absence of somatic growth, equals

$$r_{a+1,\,\max} = \frac{qc}{b^{1-\beta}L_{a+1}^{\alpha(1-\beta)}} = \frac{qc}{W_{a+1}^{1-\beta}}, \tag{5}$$

The model by Lester et al. (2004) is a special case of Eqs. (1a) and (1b), with $\beta = 2/3$, $\alpha = 3$, $q = 1$, and $r_a = r$ in adults.

2.3. Implementation considerations

A natural – if not necessary – choice for the model's time steps is the time interval separating reproductive events. Many organisms reproduce seasonally once per year, so annual time steps are typically adequate. As reproduction tends to be more frequent closer to the tropics, shorter time steps may be required there to obtain a more accurate description of the temporal patterns in the growth of such species.

The gonads mentioned in the assumptions above must be interpreted in a broad sense: what is measured by G_a is the hypothetical gonadic weight corresponding to the total energy invested into reproduction at age a. It is common to quantify the reproductive investment into gonads by the gonadosomatic index, which can alternatively be defined as the ratio $G_a/W_a = r_a$ of gonadic weight to somatic weight, or as the ratio $G_a/(W_a+G_a) = (r_a^{-1}+1)^{-1}$ of gonadic weight to total weight. When comparing this gonadic weight or gonadosomatic index to empirical observations, it must be borne in mind that in the present model these quantities include all energetic costs of reproduction, and thus all energy allocations to processes such as spawning migrations, sexual ornaments, courtship displays, competition for mates, mating behaviour, and parental care. If these costs can be quantified, and hence converted to equivalent gonadic weight and subtracted from model-predicted gonad weights, or if gonadic tissue represents the major component of energetic investment into reproduction, observed gonad weights can be compared meaningfully with the model-predicted gonad weights. In other cases, such comparisons will be difficult, and the model-predicted gonad weights, if interpreted naively, will appear unrealistically large. Furthermore, the simplifying assumption of equivalence between reproductive investments into gonadic tissue and into other costs of reproduction implies that the maintenance costs for these investments are equivalent, and in particular, that they exhibit the same allometric scaling.

Since the growth model above is process-based, temporal or inter-individual variation in resource availability can readily be incorporated. This can be achieved, for example, by considering such variation in the allometric coefficient c of net energy acquisition (e.g., Dunlop et al., 2009; Enberg et al., 2009). Evolutionary life-history models have also considered this coefficient as an evolving trait subject to a growth-survival trade-off, to reflect the possibility that faster growth may be achieved through increased risk-taking (e.g., Lima and Dill, 1990; Enberg et al., 2009; Dunlop et al., 2009; Jørgensen and Fiksen, 2010; Cressler et al., 2010; 2012).

3. Consequences of different net-intake exponents

We first illustrate that the fit of the growth model in Eqs. (1a) and (1b) to size-at-age data is often practically indistinguishable from other commonly used mathematical descriptions of growth. Thus, we start by considering a von Bertalanffy fit to the mean size-at-age of a population in which individual growth trajectories follow the growth model in Eqs. (1a) and (1b); see Kozlowski (1996) for a similar comparison. In a next step, we show that nearly identical growth trajectories can result from four net-intake exponents spanning most of the range reported for teleost fish (β=2/3, 3/4, 0.8, and 0.88); see Banavar et al. (2002) for a similar argument based on the Pütter (1920) model. We then show that the consequences of alternative values of β for reproductive investment, in contrast, are pronounced. Finally, we compare the life-history consequences of different values of β, by studying fitness as a function of age at maturation and mortality rate.

3.1. Predictions for somatic growth trajectories

As described by Lester et al. (2004) and Quince et al. (2008a), juvenile growth in length is linear for $\beta = 2/3$ and $\alpha = 3$, and close to linear for similar values of the net-intake exponent. After maturation, reproduction reduces somatic growth, and as growth approaches the asymptotic size L_∞, somatic growth ceases, since all net energy intake is then required to secure the relative reproductive investment r.

To compare the growth trajectory described by the growth model in Eqs. (1a) and (1b) with that of a von Bertalanffy model, we assume an exponent of $\beta = 3/4$ and consider a population with a normal distribution of ages at maturation with a mean of 7.5 yr and a range from 5 to 10 yr. Fig. 1 shows the resultant mean and standard deviation of size-at-age, and illustrates that the von Bertalanffy model provides a reasonable fit to these growth trajectories. A closer look reveals small systematic deviations, but in comparison with real data fraught with observation error, these deviations would often go unnoticed. We therefore conclude that the growth trajectories resulting from the growth model in Eqs. (1a) and (1b) will often be statistically indistinguishable from the von Bertalanffy model. Thus, a satisfactory fit to the von Bertalanffy model does not at all suffice to critically evaluate the specific quantitative assumptions underlying that growth model.

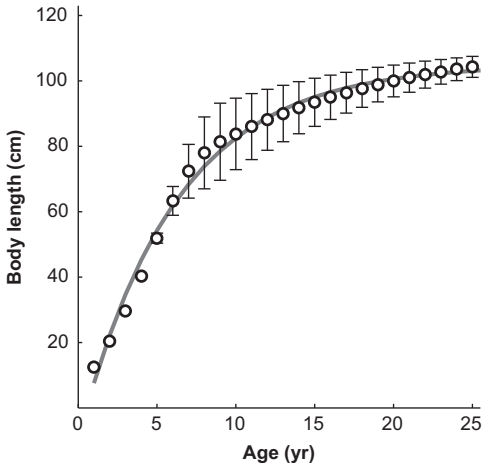

Fig. 1. Comparison of the growth model in Eqs. (1a) and (1b) with von Bertalanffy growth. White circles show the mean population growth trajectory from the growth model in Eqs. (1a) and (1b). Error bars give ± 1 standard deviation in size-at-age. The data is generated by assuming that fish mature between 5 and 10 yr old, using normally distributed maturation ages with mean 7.5 yr; growth begins to slow down during the year before first reproduction (a_{mat}) as resources are diverted to reproduction. Parameters: $\beta = 0.80$, $c = 3.08$, and $r = 0.455$. The grey line shows the von Bertalanffy growth curve (estimated parameters: $L_\infty = 105$ cm, $b = 0.163$ yr^{-1}, and $t_0 = 0.539$ yr) fitted with nonlinear least-squares regression to growth data from the growth model in Eqs. (1a) and (1b).

What is more, virtually identical growth trajectories can be obtained from the growth model in Eqs. (1a) and (1b) for different net-intake exponents. We illustrate this by comparing growth trajectories for four different values of β. These include $\beta = 2/3$, used in the von Bertalanffy growth model and in the growth model by Lester et al. (2004), $\beta = 3/4$, used in the metabolic theory of ecology (West et al., 2001; Brown et al., 2004), and $\beta = 0.80$ and 0.88, matching the empirically observed average allometric scaling of metabolic rate across teleost fishes from different studies (Clarke and Johnston, 1999; White et al., 2006; Killen et al., 2010). Assuming an age at maturation of 7 yr, the remaining parameters of the growth model in Eq. (1) can be adjusted so as to obtain practically indistinguishable growth trajectories for length (Fig. 2a), as well as for weight (Fig. 2b). From this we can conclude that it will often be impossible to estimate the net-intake exponent using size-at-age data alone (Mollet et al., 2010), even though a generally good fit between the resulting growth trajectory and observed size-at-age is obtained (compare Banavar et al. (2002)).

3.2. Predictions for reproductive investments

Despite their close agreement for somatic growth, the four considered allometric exponents give strikingly different predictions for another crucial aspect of life histories, reproductive investment at age. The highest considered exponent ($\beta = 0.88$) results in a reproductive investment that in our example is roughly twice that resulting for the lowest considered exponent ($\beta = 2/3$), with predictions for $\beta = 3/4$ and $\beta = 0.80$ falling in between (Fig. 2c). This shows that practically indistinguishable somatic growth trajectories can be associated with vastly different levels of reproductive investment, depending on the assumed net-intake exponent.

3.3. Predictions for evolutionary implications

The life-history consequences of different net-intake exponents are further emphasised when assessing their evolutionary implications. We illustrate this by comparing how net-intake exponents influence the fitness of different ages at maturation (Fig. 3).

We find that the lowest considered exponent ($\beta = 2/3$) not only results in the lowest overall expected lifetime reproductive investment, but also in the lowest evolutionarily optimal age at maturation ($a^*_{mat} = 6$ yr; Fig. 3a). Higher exponents lead to increased expected lifetime reproductive investment and favour considerably later ages at maturation ($a^*_{mat} = 9$ yr for $\beta = 3/4$, 12 yr for $\beta = 0.80$, and 20 yr for $\beta = 0.88$). A life-history model that predicts nearly identical growth trajectories can thus imply vastly different evolutionarily optimal ages at maturation, depending on the chosen net-intake exponent (see also Fig. 5B in Quince et al., 2008a).

The net-intake exponent also influences how the evolutionarily optimal age at maturation changes with the overall mortality experienced by an organism. Qualitatively, the pattern is the same for different values of β, with higher mortality rates resulting in earlier evolutionarily optimal maturation (Fig. 3c; see also Fig. 5A in Quince et al., 2008a). Not only do higher values of β lead to later evolutionarily optimal maturation, as described in the previous paragraph, but the sensitivity of a^*_{mat} with respect to natural mortality also declines at higher values of β (Fig. 3d).

These findings have practical implications for understanding altered selection pressures and their consequences in natural populations caused by anthropogenic changes in mortality regimes (Palumbi, 2001; Hutchings and Fraser, 2008; Allendorf and Hard, 2009).

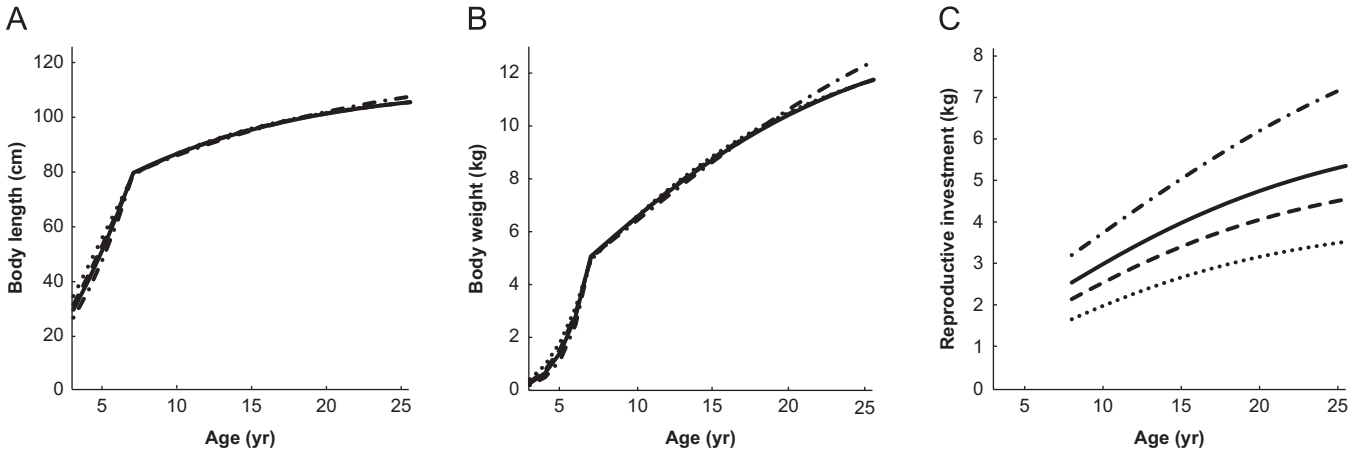

Fig. 2. Differences in reproductive investment for three similar growth trajectories with different allometric exponents for net energy intake. (A) Length-at-age and (B) body weight at age are nearly indistinguishable across the four shown parameter combinations, while (C) reproductive investment at age varies significantly. Parameters: $\beta = 2/3$, $c = 7.15$, and $r = 0.300$ (dotted line); $\beta = 3/4$, $c = 4.2$, and $r = 0.387$ (dashed line); $\beta = 0.80$, $c = 3.08$, and $r = 0.455$ (continuous line); $\beta = 0.88$, $c = 1.879$, and $r = 0.582$ (dot-dashed line); $a_{\mathrm{mat}} = 7$ yr.

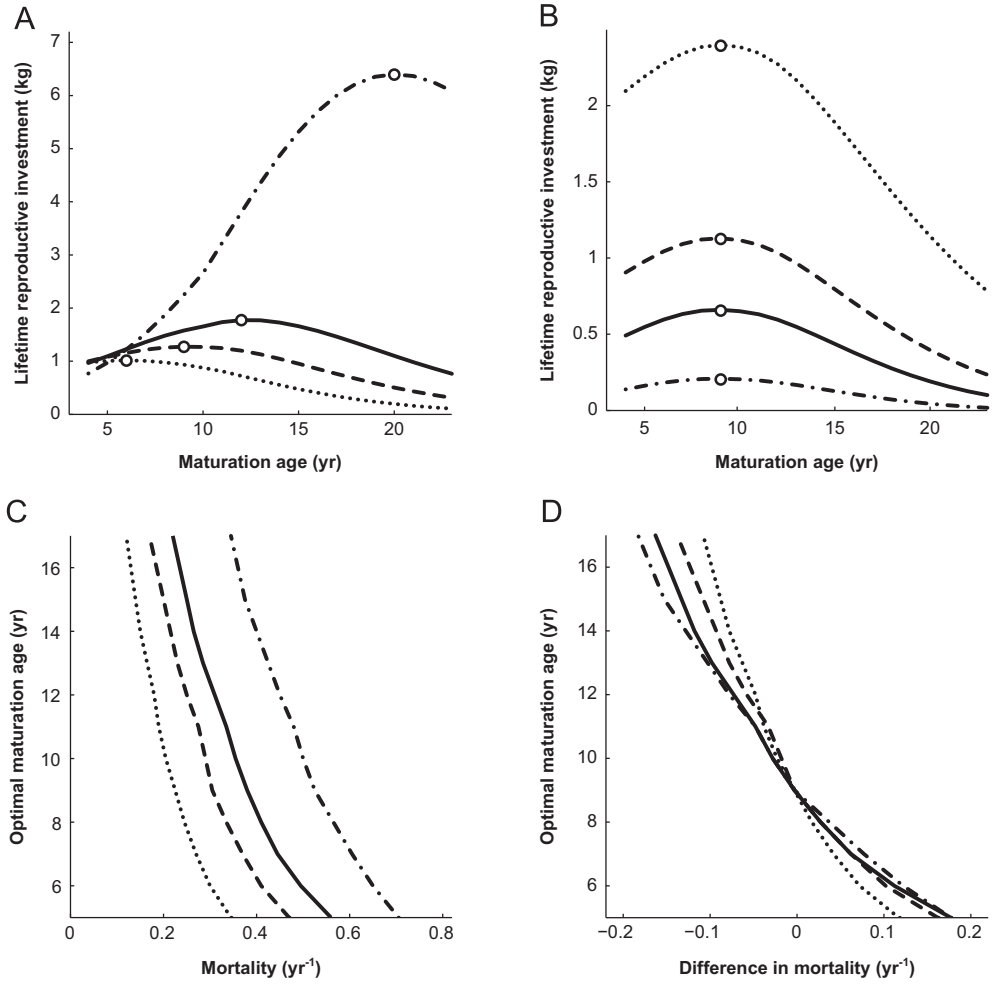

Fig. 3. Evolutionary implications of different allometric exponents for net energy intake. In all panels, the three sets of growth parameters (β, c, and r) are the same as in Fig. 2 (dotted line: $\beta = 2/3$; dashed line: $\beta = 3/4$; continuous line: $\beta = 0.80$; dot-dashed line: $\beta = 0.88$). (A) Fitness of different ages at maturation for a mortality rate of 0.3 yr^{-1}. Lines depict expected lifetime reproductive investment ("gonads") and circles indicate the evolutionarily optimal maturation age (i.e., age at first reproduction). (B) Expected lifetime reproductive investment ("gonads") at the value of mortality rate that favours an age at first reproduction of 9 yr (circles). The corresponding mortality rates are: 0.22 yr^{-1} (dotted line), 0.31 yr^{-1} (dashed line), 0.38 yr^{-1} (continued line), and 0.53 yr^{-1} (dot-dashed line). (C) Optimal age at maturation in dependence on mortality rate. (D) Sensitivity of age at maturation to changes in mortality rate; the baseline mortality for each set of growth parameters is the same as in panel B. The largest allometric exponent is least sensitive to changes in mortality rate.

In particular, for studies of fishing-induced life-history evolution (for reviews see Jørgensen et al., 2007; Dunlop et al., 2009), our results show how a wrongly estimated net-intake exponent may bias predictions of evolutionarily optimal ages at maturation (Fig. 3a); of total reproduction, and thus recruitment, in exploited stocks (Fig. 3b); and of the predicted magnitudes of evolutionary changes in maturation schedules in response to altered fishing mortality (Fig. 3c and d).

Another situation in which growth models and their evolutionary predictions may be useful is when estimates of mortality are poor or absent, as is often the case for natural populations. If in such a situation data on a population's mean growth trajectory and mean age at maturation are available, and if the population's environment has not changed considerably over a sufficient number of generations, one can attempt to estimate the total mortality rate the population experiences based on the assumption that it has adapted to express an optimal life history in the considered environment. If total mortality is roughly constant throughout life, except at juvenile stages, which may be regulated by an unspecified density-dependent process, the growth model in Eqs. (1a) and (1b) can be used to estimate the total mortality rate from the observed life history, by inverting the relationship presented in Fig. 3c. As shown in that figure, using a wrong net-intake exponent in such an analysis leads to systematically biased mortality estimates. We can illustrate this bias by considering the dependence of fitness on age at maturation for three populations in which the considered combinations of net-intake exponents β and total mortality rates M differ, and yet all result in an evolutionarily optimal age at maturation of 9 yr (Fig. 3b). If M is then estimated as described, the corresponding estimates are quite different: $M=0.22\ \mathrm{yr}^{-1}$ for $\beta=2/3$, $0.31\ \mathrm{yr}^{-1}$ for $\beta=3/4$, $0.38\ \mathrm{yr}^{-1}$ for $\beta=0.80$, and $0.53\ \mathrm{yr}^{-1}$ for $\beta=0.88$.

4. Discussion

Allometric scaling of physiological processes with body size has important consequences for life-history theory. Here we have presented a new formulation of the biphasic growth model of Quince et al. (2008a). The particular strength of this family of growth models is that it allows the allometric exponent for net energy intake to take any positive value. In contrast to Quince et al. (2008a), who used a mathematically convenient but abstract 'generalised' size to express growth, our formulation expresses size in terms of real length and weight. This makes the model more accessible and applicable. Further, we have shown the consequences of choosing different values of the net-intake exponent for somatic growth trajectories and reproductive investment at age: different exponents produce nearly identical growth trajectories, whereas the concomitant reproductive investment is highly dependent on the exponent. We have also demonstrated how these findings have important implications for life-history evolution, in particular with regard to evolutionarily optimal maturation schedules.

4.1. Allometric scaling and foraging ecology

The growth model considered here is based on the assumption that an organism's net energy intake, i.e., its gross energy intake minus its metabolic costs, is an allometric function of its current body size. An implied assumption is that the same allometric exponent applies to these two component processes. This entails hidden assumptions about the foraging ecology of the organism in question, namely that the rates of energy intake and food processing allometrically increase with body size. This may be a reasonable assumption for many predators, especially when their energy-intake rates are limited by size-based constraints that require larger predator sizes for accessing wider portions of the available spectrum of prey sizes. Typical examples of such constraints are the allometric scaling of a predator's visual acuity (McGill and Mittelbach, 2006) and gape-size limits to a predator's prey range (Aljetlawi et al., 2004; Brose, 2010; Rall et al., 2012; Klecka and Boukal, 2013). Likewise, the maximal running or swimming speeds of predators and their prey may require successful predators to be sufficiently larger than their prey (Peters, 1983; Pawar et al., 2012). Similar allometries result, for entirely different physiological reasons, also for plants, in which the capacity for light interception is often allometrically related to their height (Falster et al., 2011).

Pawar et al. (2012) showed that a consumer's search space influences the allometric scaling of its consumption rates. They concluded that the slope of consumption rate scales sublinearly with body mass (corresponding to $\beta=0.85$ in our model) for interactions that primarily take place in two dimensions, and superlinearly ($\beta\approx1.05$) for interactions in three dimensions. However, these findings are not fully consistent with predictions of life-history theory and may be confounded by methodological issues (Giacomini et al., 2013). Using the reciprocal value of handling time as a proxy of feeding rate suggests a range of ~0.1–0.75 for taxon-specific averages of the scaling exponent of the body mass-feeding rate allometry in marine and freshwater ectotherms and invertebrates (Table 1 in Rall et al., 2012).

Glazier (2006) gives an overview of intraspecific allometries of metabolic rate. Even when outliers with insufficient body-size range (less than one order of magnitude) and data with no information on size range are omitted, the metabolic-rate

Table 1
Variables, parameters, and parameter values in the growth model presented in the text. See also Quince et al. (2008a).

Subject	*Variable or parameter*	*Variable or parameter Symbol*	*Value*	*Unit*	*Symbol in Quince et al. (2008a)*
Individual state	Somatic weight	W		g	W
	Gonadic weight	G		g	G
	Length	L		cm	L
	Age	a		yr	t
Length-weight relationship	Coefficient	b	0.01	$\mathrm{g\ cm}^{-b}$	Ω
	Exponent	α	3	Dimensionless	–
Growth	Coefficient in allometric growth rate-weight relationship	c	7.15, 4.2, and 3.08	$\mathrm{g}^{1-\beta}\ \mathrm{yr}^{-1}$	ζ
	Allometric exponent in growth rate-weight relationship	β	2/3, 3/4, 0.80 and 0.88	Dimensionless	β
Reproduction	Relative reproductive investment	r	Varied	Dimensionless	g
	Conversion factor between somatic and gonadic investment	q	1	Dimensionless	γ
	Age at maturation (= age at first reproduction)	a_{mat}	Varied	yr	$T+1$ (T=last juvenile age)

exponent varies widely in ectotherms with some degree of semelparity and indeterminate growth (between approximately 0.65–1 in fishes, 0.67–1.1 in amphibians, 0.57–1.1 in lizards, 0.55–1.2 in snakes, 0.65–1.3 in jellyfish and comb jellies, 0.77–1.0 in pelagic crustaceans, 0.18–0.83 in benthic cnidarians, 0.32–0.76 in oligochaetes, 0.32–0.89 in molluscs, and 0.40–0.85 in benthic crustaceans). Similarly, the full range of intraspecific allometries in teleost fish reported by Killen et al. (2010) is 0.38–1.29. All these values indicate that the extent to which the intraspecific allometries of metabolic rate and gross energy intake are equal in individual species remains an open question. To say the least, these papers also clearly demonstrate the large potential variation in the values of the allometric scaling exponent β.

Fish show a great variety of foraging modes (e.g., Wainwright, 1991), which and can serve to highlight possible caveats of purely size-based approaches. The foraging of piscivorous fishes is typically constrained by gape size, and to some degree also by acceleration and burst swimming during an attack. Within certain limits, all of these increase with body size, and there is usually also a range of prey species (including smaller conspecifics) that a growing individual can consume (Sheldon et al., 1972; Andersen and Beyer, 2006; Brose, 2010). This is in contrast to planktivorous fishes, for which the size range of available prey is usually strictly limited, and individuals cannot choose larger prey when they grow beyond a certain size. Furthermore, manoeuvrability at the scale required to capture plankton may decrease, and time to handle small prey may therefore increase with size, such that there is an optimal size above which gross intake rate declines (Persson et al., 1998 and references therein). Planktivorous foraging has been extensively studied within the framework of physiologically structured population models (Persson et al., 1998; de Roos, 1996, 2006; de Roos and Persson, 2001), and it has been shown that the allometric scaling of planktivore foraging rate has implications for individual growth and population dynamics (Persson et al., 1998; Persson and de Roos 2006), ecosystem structure (Persson et al., 2007), and fisheries management (Van Leeuwen et al., 2008).

Quince et al. (2008a) discussed optimal growth patterns when net production is unimodal due to differences in the allometric scaling of gross energy intake and metabolic costs. They show that when these differences are small, the resulting growth trajectories are very similar to those predicted by the growth model discussed in this paper. When metabolic costs scale with a much larger exponent than gross energy intake, the general model proposed by Quince et al. (2008a) predicts nearly determinate growth, which is not in line with the prolonged period of growth after maturation in many reptiles, molluscs, and most fish species. This suggests that either the assumption of approximately equal exponents of gross energy intake and metabolic costs is satisfied, or that some additional mechanisms favouring post-maturation growth, such as size-dependent maternal effects (Sogard et al., 2008), are important in shaping their life histories, and consequently, should be included in evolutionary models developed for these organisms.

4.2. Significance of net-intake exponent for life-history modelling

There have been many calls for moving beyond the standard von Bertalanffy growth curve, for both statistical and biological reasons (e.g., Roff, 1980; Day and Taylor, 1997; Czarnoleski and Kozlowski, 1998). The continual use of the standard von Bertalanffy growth curve is somewhat paradoxical because von Bertalanffy (1938) himself explicitly considered the effects of different values of the allometric scaling exponent for energy intake on growth trajectories and showed that the exponent crucially affects the predicted growth. Our analyses further suggest that, regardless of the choice of growth model, the value used for the net-intake exponent plays a more important role than has been previously recognised, because it strongly affects the predicted reproductive investment.

In life-history modelling, both size-at-age and reproductive investment matter. This issue has gained new importance due to the recent efforts to model contemporary evolution, and particularly fishing-induced life-history evolution, where reproductive investment is essential for determining fitness (e.g., Law and Grey, 1989; Dunlop et al., 2009). Our analysis suggests that the choice of growth model and of allometric exponent might influence the predicted evolutionary rate, as well as the expected magnitude, of evolutionary change. To our knowledge, no comparative study of the evolutionary consequences using different exponents exists at present, apart from Quince et al. (2008a) and the sensitivity analysis in Jørgensen and Fiksen (2010). Models used for species-specific case studies of life-history evolution are usually rather complex and difficult to compare directly. For example, Andersen and Brander (2009) and Dunlop et al. (2009) used $\beta = 2/3$, Enberg et al. (2009) used $\beta = 3/4$, and Jørgensen et al. (2006) used $\beta \approx 0.8$, while de Roos et al. (2006) modelled a planktivorous species in which net energy intake emerges from several processes with different allometric scaling.

4.3. Empirical estimation of net-intake exponents from data on body size

The size dependence of net-intake exponents could be estimated directly when appropriate experimental evidence is available, e.g., from experiments examining the shape of the functional response (Rall et al., 2012) and size-dependent consumption rates (Pawar et al., 2012). In addition, the value of the scaling exponent β could be derived indirectly from data on individual growth. This could be particularly useful for populations with detailed records of individual body sizes, as are available, e.g., for many commercially exploited fish species. Assuming that growth follows the model described here, and that many of the parameters stay constant throughout life, there are fundamentally two types of data one could use to estimate the scaling exponent β.

The first option is to focus on size-at-age data, where different exponents lead to different curvatures of growth trajectories. This effect is easiest to observe during the immature phase, when allocation to reproduction does not confound the picture. Size-at-age data routinely collected from fished populations provide a good example, as such fisheries data may contain the observations required. However, a number of factors may render such analysis difficult, or even invalid. Complicating factors include the sampling biases, niche shifts, and other ontogenetic changes that influence energy acquisition and thus growth, selective mortality (in particular size-selective mortality), and environmental fluctuations that cause further variation in the data. The signal from the exponent β on curvature is small (see Fig. 2a and b), which makes all aforementioned issues serious concerns. Furthermore, for many species the immature period is short, making it difficult to detect curvature in juvenile growth trajectories.

The second option is to use size-at-age information from fisheries data in combination with gonad size or other measures of reproductive investment. Some fisheries surveys routinely measure gonads, and can thus provide empirical observations of both somatic and gonadic investment. The value of β can be fitted to such data, as the exponent causes large variation in the expected reproductive investment. However, the total energetic costs of reproduction can be very difficult to quantify. Measures such as the gonadosomatic index provide only a lower limit (even more so for batch spawners), may be very sensitive to the timing of the measurement, are subject to the uncertainty of the mass-

energy conversion coefficient (Gunderson and Dygert, 1988), and convey no information of costs other than gonadic investments.

Size-at-age and reproductive investment can also be measured experimentally, and one can even quantify the underlying processes of gross energy intake and metabolic loss. An advantage of an experimental approach is that the allometric exponents for acquisition and metabolism could be disentangled and quantified independently. Obvious challenges are to obtain observations over a large enough size range and to provide close-to-natural conditions in a laboratory. Experimental determination of these relationships also has the advantage that environmental influences, e.g., from temperature, can be quantified and incorporated in the growth model.

Mollet et al. (2010) showed how to apply the nonlinear statistical fitting of a bioenergetic model to individual growth trajectories back-calculated from otoliths. Although they used a different growth model, their study illustrates an approach that could also estimate the parameters of the growth model presented in this paper. Mollet et al. (2010) combined immature and mature data, which requires either information on individual maturation or, as in their case, fitting of individual maturation as part of the analysis. Population-level maturity data could have been used, but this would introduce a bias that is difficult to quantify: maturation is generally size-dependent, which biases the mean growth of immature fish downwards and that of mature fish upwards in age classes in which maturation occurs. Still, combining process-based models with empirical observations can help estimate central parameters that could advance life-history modelling, as well as fisheries science and management.

5. Conclusions

Models of individual growth commonly assume a fixed allometric scaling exponent of net energy intake. For fish, this exponent is frequently taken to equal 2/3, despite limited empirical support (Pawar et al., 2012; Rall et al., 2012). Recent meta-analyses have further revealed that this exponent may vary widely within various taxa. In this study, we have shown that the exact value of this allometric scaling exponent can have profound consequences for individual fitness, optimal life histories, and population growth. Scientists now strive towards deeper levels of understanding of dynamics in aquatic ecosystems, and it is hence becoming increasingly important to make more accurate and reliable predictions about fitness, reproduction, population dynamics, and trophic interactions. Based on the results in this paper we therefore call for greater awareness of the importance of the allometric scaling exponent of net energy intake, a higher degree of preparedness to consider alternative values, and more effort to estimate the value of this important parameter in specific settings.

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